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A COMPARATIVE MORPHOLOGICAL STUDY OF THE TERMINALIA OF MALE CALYPTERATE CYCLORRHAPHOUS DIPTERA AND THEIR ACALYPTERATE RELATIVES.

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In the following discussion, especial attention has been given to the Diptera of medical and veterinary importance, and to those of economic importance as well, since these forms are of more general interest, and are more easily obtainable for study, in case one wishes to verify the evidence here presented by examining the insects themselves.

A comparative morphological study of the terminalia of certain male Diptera which are much less modified than the Calypterate Cyclorrhapha, has also been included in this discussion, in order to present the highly important morphological evidence upon which the interpretation of the terminal abdominal structures of the higher Diptera here discussed, was based, since this interpretation is not the one usually accepted by other investigators—and, in fact, there is no "current" interpretation of the parts in general use among recent students of the Diptera, each of whom appears to have his own views on the subject, differing from those of other investigators in this field.[1] Past experience has shown that the method of comparative

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[1] Snodgrass, 1935, for example, considers that the forcipate parameres of the lower Diptera represent the "coxites and styli" of male Thysanura, and assigns the sixth sternite to the eighth segment (whose tergite is supposedly represented by the pregenital plate) since he considers that the sixth segment has apparently become obliterated in male Cyclorrhapha. Patton, 1932–1935, and his students, on the other hand, consider that the eighth, rather than the

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morphology, involving the study of an ascending series of intergrading lower forms leading to the higher ones, is the most productive of satisfactory results, in attempting to interpret the morphological structures developed in the higher forms such as the Calypterate Cyclorrhapha; and this method is therefore the one adopted here, although the method of comparative morphology is not held in high esteem by many recent investigators, who prefer to reach their conclusions by other lines of reasoning.

The writer is firmly convinced that the modifications exhibited by the male terminalia, which, in the higher Diptera, include features of not less than seven segments of the abdomen (i.e., the fifth to the eleventh, inclusive), are of prime importance, not only for the identification of species, but also for indicating the natural affinities and the family groups to which these Diptera belong. In fact, as is discussed later on, even such a brief study as the present one clearly indicates that some of the accepted family groupings (which are frequently based upon such minor features as the vestiture, etc.) need revising; and if the highly important study of the male terminalia is to add its evidence to that from other sources, for determining the natural affinities of the Diptera, it is evident that some effort should be made to homologize the parts correctly throughout the series of forms to be studied from the standpoint of comparative morphology.

In contrasting the male terminalia of the higher Diptera with those of the lower Diptera, we may note the following differences. The clasping organs of typical male Nematocera are segmented parameres (labeled *bm* and *dm* in Figs. 1 and 2), which work in and out laterally; and the aedeagus is directed more nearly backward in these Diptera, even when the ninth segment (and frequently the eighth also) undergoes a rotary inversion, as is the case in certain Tipulidae, Tanyderidae, Psychodidae, Culicidae, Mycetophilidae, etc., among the Nematocera, and in certain Asilidae, Bombyliidae, Cyrtidae, etc., among the Orthorrhaphous Brachycera. In most Cyclorrhapha, on the other hand (and in some of their near relatives

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sixth, abdominal segment has become obliterated in male Cyclorrhapha (following Awati, 1915, in this matter) and interpret the surstyli and connecting rods as the "coxites and styli" in the higher Diptera, while Cole, 1927, considers that the pregenital plate is formed by the seventh and eighth "tergites," while the sixth sternite supposedly represents the eighth sternite in the higher Diptera according to his interpretation, which is accepted by many recent Dipterists.

among the Orthorrhaphous Brachycera), the clasping organs, which may be formed by the gonapophyses, surstyli and cerci (labeled *a, b, st* and *ce* in Fig. 11) work backward and forward, and the aedeagus, *ae,* is directed forward and downward (instead of posteriorly), due to the more or less complete circumversion of the ninth segment[2] (and the parts behind it) in practically all male Cyclorrhapha. The sixth, seventh and eighth abdominal sternites (labeled *6s, 7s* and *8s* in Fig. 3 to 11, inclusive) may form an oblique series extending up the insect's left side in male Cyclorrhapha; but such an arrangement of the parts does not occur in male Nematocera, or in the lower Brachycera, although a suggestion of this modification is exhibited by such Dolichopodidae as *Argyra* (described by Crampton, 1941); and some Bombyliidae, Cyrtidae, etc., exhibit a tendency toward a torsion of the parts characteristic of most male Cyclorrhapha (as is also the case in the "borderline" families Lonchopteridae and Phoridae).

The stages passed through in the development of the modifications exhibited by the terminalia of the higher Diptera are illustrated by the series of Diptera shown in Figs. 1 to 11, inclusive.

In the Tipulid *Cladura* (Fig. 1), the ninth segment (*9t* and *9s*) is large, and the backwardly-projecting, two-segmented, forcipate parameres (*bm* and *dm*) are large and distinct. The eighth sternite, *8s,* although slightly reduced, remains much larger than the eighth tergite, *8t,* which tends to become vestigial, even in this primitive Nematoceran; and the tendency for the eighth tergite to become vestigial, and eventually to become obliterated, is increasingly apparent as we pass through the series leading to the higher Diptera.

In the Stratiomyid *Ptecticus* (Fig. 2) the ninth segment remains large and well developed (due to the fact that it bears the intromittent organ necessary for the continuation of the species), and is capable of being twisted forward during the copulatory movements, due to the development of the membranous conjunctivae between it and the preceding segments. The distal segments of the forcipate

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[2] The circumversion of the ninth segment results in the looping up of the ejaculatory duct over the top of the hindgut (see Fig. 54), from left to right, in every male Cyclorrhaphan thus far examined (including the Syrphidae and other ancestral Cyclorrhapha), and this looping will doubtless be found to occur in male Bombyliidae, Cyrtidae, Phoridae, Lonchopteridae, and other Orthorrhaphous Brachycera whose lines of descent approach that of the Cyclorrhapha.

parameres, *dm,* become reduced to short flat structures (somewhat suggestive of similar structures occurring in the Syrphid *Syrphus rectus,* described by Crampton, 1941), and the basal segments of the parameres (*bm* of Fig. 2) unite basally with the ninth sternite, *9s,* as they do in the males of many other Diptera.

The eighth tergite, *8t,* remains vestigial in *Ptecticus* (Fig. 2); and the reduction tendency extends forward to include the seventh tergite, *7t,* as well, in the stage of development illustrated by *Ptecticus,* since both tergites have now become reduced to narrow transverse bands, although their corresponding sternites are not so greatly reduced as the tergites are. The seventh and eighth segments thus become differentiated from the preceding segments to form a sort of postabdomen, characteristic of the higher Diptera. In this Stratiomyid (Fig. 2) the eighth sternite, *8s,* is capable of twisting slightly upward into the insect's left side, at least temporarily during mating; and this tendency toward the temporary lateroversion of the eighth sternite (and its ultimate permanent inversion in the higher Diptera) becomes unmistakably apparent as we trace its modifications through the actual ancestral series (i.e., the Cyrtids and their allies) leading to the higher Diptera (Fig. 3) although merely a suggestion of the lateroversion tendency is hinted at in such insects as *Ptecticus* (Fig. 2), which are not in the direct line of descent of the Syrphoid Cyclorrhapha (although some investigators consider that the Syrphidae were derived more or less directly from the Stratiomyidae).

As will be discussed in a later paper dealing with the terminalia of male acalypterate Cyclorrhapha, certain Cyrtidae furnish excellent prototypes foreshadowing the development of the Syrphid and Pipunculid types next to be considered; and in these Cyrtids, the sixth tergite (as well as the seventh and eighth tergites) becomes a narrow transverse band, while the corresponding sternites remain fairly large and well developed, as they are in the Syrphoidea. In these Cyrtids, the seventh and eighth sternites become drawn up, to some extent, into the insect's left side, as the ninth segment becomes inverted, by revolving, from left to right, through 180 degrees, about the long axis of the body; and this rotary inversion of the ninth segment is a preliminary developmental stage, preceding the folding forward of the ninth segment against the insect's right side, which is characteristic of the insects next to be considered.

In the next stage of the series, illustrated by the Syrphid *Heliophilus* shown in Fig. 3, the ninth segment, *9s* (which had apparently previously undergone a preliminary rotational inversion), now becomes folded forward against the insect's right side. Since the ninth segment of *Heliophilus* (Fig. 3) does not thereafter begin a circumversion movement, as it starts to do in the next stage illustrated by the Syrphid *Sericomyia* shown in Fig. 4, the relatively slight movements of the ninth segment do not result in an appreciable traction to cause the eighth sternite to become drawn up into the insect's left side in *Heliophilus* (Fig. 3), so that the large relatively unmodified eighth sternite, *8s,* of Fig. 3, still remains in line with the other sternites, *6s* and *7s,* forming a normal chain of ventrally located sternites, almost exactly like the corresponding sternites, *6s, 7s* and *8s,* of the normally developed Stratiomyid shown in Fig. 2, in which no one would deny that all of these sternites are actually such, instead of representing "displaced tergites," as they are usually interpreted in the higher Diptera. Thus, if comparative morphology has any meaning at all, it is quite evident that it is the *tergites* (and *not* the *sternites*) of the eighth and seventh segments which exhibit an unmistakable tendency to become vestigial or atrophied as we trace their development in the Cyclorrhapha; and the significance of such trends is quite obvious to anyone familiar with the method of comparative morphology for tracing the significance of the modifications later occurring in the higher Diptera derived from ancestors not very different from the forms just described.

As was mentioned above, the initial stages leading to the modifications exhibited by the terminalia of male Cyclorrhapha are: first, a clockwise rotation of the ninth segment about the long axis of the body, through 180 degrees, resulting in the inversion of the ninth segment (with the proctiger); next, a forward-folding of the ninth segment against the insect's right side, as shown in Fig. 3. The ninth segment now begins to execute a "circumversion" movement, which is arrested in various stages of completion in different Syrphidae. Thus, in the Syrphid *Sericomyia,* shown in Fig. 4, the ninth segment has started on a "circumversion" movement and now hangs down ventrally and faces somewhat to the left, instead of facing anteriorly as in Fig. 3. This added twisting around of the inverted ninth segment brings about an increasing pull upon the neighboring eighth sternite, *8s* of Fig. 4, which causes the latter to become drawn still further upward into the insect's left flank. The sixth and seventh sternites, *6s* and *7s* of Fig. 4, likewise tend to follow the lead of the eighth sternite, *8s,* which precedes them in the upward migration into the insect's left side, due to the fact that the eighth sternite is the one next to the gyrating ninth segment, and is consequently the first to be influenced by its traction, and is pulled further upward by its gyrations. As the ninth segment, *9t,* swings still further around in the Syrphid *Paragus* shown in Fig. 6, the eighth sternite, *8s,* is twisted correspondingly further upward into the dorsal region (since there is nowhere else for it to go if the twisting movement continues), where it becomes practically inverted; and the eighth sternite, *8s,* finally becomes completely inverted in the Syrphid *Baccha* shown in Fig. 5, in which the ninth segment, *9t,* has now practically completed its circumversion movement.

It is very significant that the eighth sternite, *8s,* always lags behind the ninth segment, *9t,* in the twisting movements, being but little disturbed when the gyrations of the ninth segment are slight (as in Fig. 3), and becoming inverted only when the ninth segment has practically completed a drastic circumversion movement, as in Figs. 5 and 6, thus indicating that the eighth sternite does not execute a circumversion movement when the ninth segment does, in male Cyclorrhapha. It is also highly significant that the ninth segment is always free of, and separated from, the eighth sternite, as the ninth executes its independent maneuvers (in Figs. 3 to 6); and although the ninth segment, *9t,* severs its connections with the eighth sternite, *8s,* the latter always remains in close connection with its preceding fellow sternite, *7s,* and tends to form an increasingly closer union with it (in Figs. 5 and 6), as we would expect it to do, if the plate, *8s,* is a sternite, instead of a tergite.

The above-mentioned Syrphidae are by no means the only lower Cyclorrhapha illustrating with almost diagrammatic clearness the successive stages resulting in the inversion of the eighth sternite (as the oblique upward twist of the sternites follows the gyrations of the ninth segment), since the writer has found excellent illustrations of the torsion of the parts in the lower Pipunculidae (which will be described later in another paper dealing with the lower Cyclorrhapha), and Dr. D. Elmo Hardy has very kindly called the writer's attention to a fine series of male Pipunculidae (or "Dorilaidae") in which the torsion of the terminalia can be traced from such genera as *Chalarus, Prothechus, Nephrocerus* and *Cephalosphaera,* up through *Dorilas* and *Tomosvaryella,* thus demonstrating the torsion of the sternites very conclusively to anyone who is willing to accept the evidence of comparative morphology in this matter. Males of these Pipunculidae, however, are much rarer and more difficult to obtain for study than is the case with the above-mentioned Syrphidae, which will serve equally well for such a study, if one wishes to examine the insects themselves, in order to test the validity of the conclusions here expressed concerning the interpretation of the parts of the terminalia of male Cyclorrhaphous Diptera.

In evident accord with the adumbrational features exhibited by the members of other ancestral groups, the modificational trends exhibited by certain members of the "ancestral" Syrphid series may foreshadow those later developed to a still higher degree in the Cyclorrhapha descended from Syrphid-like ancestors. Thus, for example, in the Syrphid shown in Fig. 6, there is a pronounced tendency for the lateroverted seventh sternite, *7s,* to merge with the inverted eighth sternite, *8s,* to form a single composite pregenital plate;[3] and this tendency is still further intensified in the higher Cyclorrhapha shown in Figs. 9 and 10, until finally in Fig. 11, the two sternites have merged so completely to form a single pregenital plate, that its composite character is revealed only by tracing its development through the preceding series of forms leading up to it. Similarly, the tendency for the sixth sternite, *6s,* to become pronouncedly asymmetrically developed, and to become shifted into the insect's left side, in the higher Cyclorrhapha shown in Figs. 8, 9 and 10, is clearly foreshadowed in the Syrphid shown in Fig. 6.

The modificational trends exhibited by the Syrphid shown in Fig. 5 are still more like those characteristic of the higher Cyclorrhapha shown in Figs. 7 to 11, in that the ninth segment, *9t,* of the Syrphid shown in Fig. 5, undergoes a "complete" circumversion, and becomes hardened or set in this position, as it does in the higher Cyclorrhapha. Similarly, the sixth, seventh and eighth abdominal sternites, *6s, 7s* and *8s,* of Fig. 5, form an oblique series extending up the face of the insect's left flank, as they do in the higher Cyclorrhapha shown in Figs. 9 and 10, etc.; and the sixth abdominal tergite, *6t,* of the Syrphid shown in Fig. 5, is strikingly like the sixth abdominal tergite, *6t,* of the higher Cyclorrhapha shown in Figs. 7 and 10, etc., in form, position and development. In fact, the Syrphid shown in Fig. 5 furnishes an ideal starting point for tracing the modifications occurring in the series of higher Cyclorrhapha shown in Figs. 7 to 11; and it is quite possible that the lines of descent of these Cyclorrhapha arose from similar ancestors in the common Syrphid-Pipunculid ancestral stock.

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[3] The pregenital plate may be referred to as a synurite, or fusion product of two urites (abdominal segments), although it is here interpreted as a synsternite, or fusion product of two sternites, while other investigators interpret it as a syntergite, or fusion product of two tergites.

The "ancestral" character of the key group Syrphidae, in relation to the other members of the Cyclorrhaphous families descended from Syrphid-like ancestors, is indicated by the relatively primitive character of their mouth parts, and their wing venation, in addition to the more primitive condition retained by their terminal abdominal segments, in which, for example, the seventh sternite, *7s,* and the seventh tergite, *7t,* of such a Syrphid as *Sericomyia chrysotoxoides* shown in Fig. 4, remain separate and distinct, and are comparatively normally developed, with normally developed spiracles, etc., unlike the highly specialized condition exhibited by these structures in other Cyclorrhapha (Figs. 7 to 11)—as would naturally be expected in the Syrphids, which occupy a position at the base of the lines of descent of the Cyclorrhapha in general, and furnish the key for interpreting the modifications met with in the higher Cyclorrhapha. The Syrphidae themselves, together with the Pipunculidae and Conopidae, are grouped in the superfamily Syrphoidea, here referred to as the ancestral Syrphoid stock, since the actual ancestors of the Cyclorrhapha (descended from the Cyrtidae) were doubtless sufficiently closely related to the members of the Syrphoidea to be included in the same superfamily with them.

The Ortaloid series (including the Pyrgotidae, Ortalidae, Trypetidae, Richardiidae, Piophilidae, etc.) merges so intimately with the Syrphoid series that it is practically a direct continuation of the Syrphoid series; and the related Helomyzoid series (including the Clusiidae, Helomyzidae, etc.) may have arisen from the same Syrphoid ancestors, since its members have also retained many features suggestive of a Syrphoid origin. The members of the Helomyzoid series have likewise developed certain modificational trends suggestive of those which become more pronounced in the Calypteratae (using this term in the broader, more inclusive sense, without reference to the degree of development of the calypteres in its members), so that the members of the Helomyzoid series may be regarded as morphologically intermediate between the ancestral Syrphoid stock and the Calypteratae, without necessarily implying that the Calypteratae were derived directly from Helomyzoid forebears.

The Clusiid *Clusia lateralis* shown in Fig. 7, and the Helomyzids *Neoleria crassipes* and *Anorostoma marginatum* shown in Figs. 8 and 9, are transitional Helomyzoidea resembling both the ancestral Syrphoids and the lower members of the Calypteratae. These Helomyzoids resemble the Syrphid shown in Fig. 5, in the character of the ninth segment (which undergoes a circumversion in both types of insects), and in the oblique arrangement of the sixth, seventh and eighth sternites; and the sixth tergite of the Helomyzoids shown in Figs. 7 and 8 is very like that of the Syrphid shown in Fig. 5. On the other hand, these Helomyzoids likewise resemble the Anthomyids *Eremomyoides cylindrica* shown in Fig. 10, or *Hylemyia spiniventris* shown in Fig. 23 (both of which belong to a family occupying a position at the base of the Calypterate stem) in the general character of the ninth segment, and in the oblique arrangement of the sixth, seventh and eighth sternites; and the sixth tergite of the Helomyzoid shown in Fig. 7 is very like that of the Anthomyid shown in Fig. 10. By thus making use of the "transitional" stages furnished by the intermediate Helomyzid series illustrated in Figs. 7 to 9, we can readily trace the modifications exhibited by the Calypteratae shown in Figs. 10 and 11, back to their prototypes in the "ancestral" Syrphids shown in Figs. 3 to 6, in which it is a comparatively easy matter to identify the parts of the male terminalia.

Although the Anthomyidae (which occupy a position at the base of the Acalypterate stem) could readily be derived from Helomyzoid precursors in the manner suggested above, a Helomyzoid origin for all of the Calypteratae is not so readily apparent if the Cordyluridae (which are regarded as very primitive Calypteratae by many recent Dipterists) are likewise included in the Calypterate group, since the Cordyluridae appear to lead back to some type of precursors slightly different from those included in the Helomyzoid series.

Such Cordylurids as the one shown in Fig. 17 (*Parallelomma*) or the one shown in Fig. 16, have surstyli, *ss,* very like the surstyli of the Ephydrid *Ochthera mantis,* and a large sixth tergite, *6t,* is retained in these Cordylurids, as is also the case (?) in the Ephydrid *Ephydra millbrae,* figured by Cole, 1927. This, however, does not necessarily imply that the Cordyluridae arose from ancestors related to the Ephydridae, since the Cordyluridae likewise resemble the members of the superfamily Calobatoidea (including the Micropezidae, Calobatidae, Neriidae, etc.) much more closely in the character of their terminal abdominal structures, etc.

Thus, the entire sixth abdominal segment is characteristically large and normally developed in such Calobatoids as those shown in Figs. 14 and 15; and the sixth abdominal tergite, *6t,* is also large and well developed in the Cordylurids shown in Figs. 16 and 17. The large, distinct, lateroverted seventh sternite, *7s* (which is not accompanied by the sixth sternite, *6s,* in its migrations), of the Calobatoids shown in Figs. 14 and 15 is quite suggestive of the type of seventh sternite, *7s,* occurring in the Cordylurids shown in Figs. 16 and 17; and the downwardly-bent ninth segment, with its forwardly-directed aedeagus, *ae,* in the Calobatoids shown in Figs. 14 and 15, is very suggestive of these structures in the Cordylurids shown in Figs. 16 and 17. Furthermore, the fifth sternite tends to send down large, peculiarly-formed ventral processes in both of these groups of Diptera, and the modifications exhibited by the terminalia of male Cordylurids are thus very suggestive of an origin in some Calobatoid ancestry. In fact, if the large sixth tergite, *6t,* of the Calobatoid shown in Fig. 15, (compare also Fig. 14) were to become shifted backward, and the reduction of the sixth sternite, *6s* (already begun in this Calobatoid), were to continue during the backward shifting of the sixth segment, a type of male terminalia extremely like that found in the Cordylurids shown in Figs. 16 and 17 would be produced, thus suggesting that the Cordylurid members of the Calypteratae might have been derived from Calobatoid forebears among the Acalypteratae, although the final solution of the problem of the origin of the Calypteratae, as a whole, must evidently await further study before this problem can be definitely solved.

The Scatophagidae are placed in the family Cordyluridae, among the primitive Calypteratae, by many recent Dipterists; but the terminalia of a typical male Scatophagid, such as the one shown in Fig. 18, for example, do not resemble the terminalia of the Cordylurids shown in Figs. 16 and 17, anywhere nearly as much as they do the terminalia of typical male Anthomyids, such as those shown in Figs. 19 and 10. Thus, the "vertical" sixth tergite, *6t,* of the Scatophagid shown in Fig. 18, resembles the "vertical" sixth tergite, *6t,* of the Anthomyid shown in Fig. 10, rather than the elongated "incumbent" sixth tergite, *6t,* of the Cordylurids shown in Figs. 17 and 16; and the displaced sixth sternite, *6s,* located directly under the vertical pregenital plate, *7s* and *8s,* of the Scatophagid shown in Fig. 18, is much more suggestive of these parts in the Anthomyid shown in Fig. 19, than is the case with the same structures in the Cordylurids shown in Figs. 17 and 16. Similarly, the posteriorly-directed ninth segment, *9t,* and the appendages labeled *st* and *ce* in the Scatophagid shown in Fig. 18, are much more like the posteriorly-directed ninth segment, *9t,* and the appendages, *st* and *ce,* in the Anthomyid shown in Fig. 19, than is the case with the downwardly-directed ninth segment, *9t,* and the peculiar surstyli, *st,* etc., of the Cordylurids shown in Figs. 16 and 17, so that so far as the evidence of male terminalia is concerned, these Scatophagids seem to be more closely related to the Anthomyidae, than to the Cordyluridae.

The Glossinidae, such as *Glossina* sp., shown in Fig. 22, have preserved a large distinct normal sixth tergite, *6t;* and the narrow sixth sternite, *6s,* appears to merge with the vertical pregenital plate, *7s* and *8s,* above it, in a fashion very suggestive of the condition exhibited by the Scatophagid shown in Fig. 18, and the arrangement of the parts is likewise not very different from that exhibited by the Anthomyid shown in Fig. 19. These facts may possibly be taken to indicate that the Glossinidae arose from the common Anthomyid stock, which gave rise to the Scatophagidae as well.

The Anthomyids are among the most primitive representatives of the Calypteratae and form a key group upon which many other Calypterate families converge. They apparently intergrade with the Scatophagidae on the one hand, and with the Muscidae on the other, which might be taken to indicate that all of these forms should be placed in a single family; but since they fall into groups as distinct as those usually regarded as families by the students of the higher Diptera, these groups may be regarded, for convenience, as representing separate "families" of very closely related Calypteratae.

Most Anthomyidae (or Anthomyiidae, as the name is properly spelled) have a deeply cleft fifth sternite, *5s,* with well-developed copulatory lobes, *cl,* as in the Anthomyids shown in Figs. 34, 25, 23, 19, 10, etc.; and the surstyli, *st,* are usually long and slender in typical members of this family (for a description of the surstyli, etc., see the further discussion of these parts under the description of the terminal structures of the Calliphoridae). When the above-mentioned structures are not typically developed in the Anthomyidae (as in Fig. 29), the area belonging to the lateroverted seventh sternite, *7s,* of Fig. 29, is usually large and well demarked in a fashion not found in most members of the other families related to the Anthomyidae. The sixth tergite, *6t,* is usually fairly large and distinct in the Anthomyids, such as those shown in Figs. 10, 23, 26, etc., but when the sixth tergite is not distinct, the sixth sternite, *6s,* may become large and form a stout loop about the posterior border of the cubiculum (or pouch into which the aedeagus is thrust in repose), as is the case of the Anthomyid shown in Figs. 24 and 25.

In the very primitive Anthomyid *Hylemyia spiniventris* shown in Fig. 23 (which is enough different from *Hylemyia antiqua* shown in Fig. 34, to be placed in a different genus, "Protohylemyia") the lateroverted seventh sternite, *7s,* is hugely developed and is distinctly demarked from the eighth sternite, *8s,* by a well-developed cleft and by a distinct, though incomplete suture. In fact, *Hylemyia spiniventris* is so very primitive in the character of its large, well-demarked seventh sternite, *7s* of Fig. 23, that it would have been better to select it, rather than the Anthomyid shown in Fig. 10, for comparison with the similarly modified Helomyzid shown in Fig. 9, but the Anthomyid shown in Fig. 10 exhibits a more marked tendency toward the reduction of the seventh sternite, and is therefore a better intermediate type leading to the stage illustrated in Fig. 11, in which the seventh sternite, *7s*, is practically obliterated.

Although some doubt has been expressed concerning the closest affinities of *Limosia errans,* shown in Fig. 31, its terminalia indicate that it is fairly closely related to such Anthomyids as *Paregle cinerella,* shown in Fig. 28. It is possible that the narrow, anterior, transverse marginal strip along the front border of the pregenital plate, *8s* of Fig. 31, of *Limosia,* may represent the very similar, though distinct, sixth tergite, *6t* of Fig. 28, of *Paregle;* and if this is the case, it would appear that in some cases the sixth tergite may unite with the pregenital plate, instead of becoming atrophied, when the sixth tergite is no longer recognizable as a distinct sclerite.

Fannia canicularis, shown in Fig. 29, is placed in the family Anthomyidae by some Dipterists, while others place it in the family Muscidae. The fifth sternite is not cleft posteriorly in *Fannia* but it lacks the characteristic small posterior processes, *cl,* borne on the hinder margin of the fifth sternite, *5s,* of typical Muscids such as those shown in Figs. 30, 32, 33, etc., and the large, well-demarked seventh sternite, *7s,* is much better developed and extends much further dorsad in *Fannia* (Fig. 29), in a manner more suggestive of the condition exhibited by the Anthomyids shown in Figs. 23, 19, etc., than is the case with the small, poorly demarked area representing the seventh sternite, *7s,* in the typical Muscids shown in Figs. 30, 32, etc. On the other hand, the surstyli, *st,* etc., of *Fannia* (Fig. 29) are not the long slender type of structures that they are in typical Anthomyids, such as those shown in Figs. 24, 28, 34, etc., although the surstyli, *st,* of *Fannia* are very like those of the less typical Anthomyid shown in Fig. 23. The terminalia of *Fannia* might permit the placing of *Fannia* in either of the two families Anthomyidae or Muscidae, but the general evidence seems to be more in favor of regarding it as an Anthomyid than as a Muscid. At any rate, a study of the terminalia of *Fannia* bears out the evidence from other sources that the Anthomyidae are closely connected with the Muscidae (as well as with the Scatophagidae). *Fannia* is likewise of interest in that the area of the pregenital plate belonging to the seventh sternite, *7s,* of this insect (Fig. 29) bears the sinistral spiracle of the sixth segment as well as its own left spiracle, and this may possibly be taken to indicate that the missing sixth tergite has united with the pregenital plate in *Fannia;* but the significance of the location of the sinistral spiracles of this region will be taken up more at length, under the discussion of these spiracles in the Tachinoid series of Calypteratae.

The typical Muscidae exhibit the following characters, which may be of some diagnostic value for determining the closest affinities of certain true Muscidae, such as *Ophyra leucostoma,* etc., which have been wrongly placed in other families by recent Dipterists.

In the typical Muscidae shown in Figs. 30, 32, etc., the fifth sternite, *5s,* is not cleft posteriorly, and the copulatory lobes, *cl,* are reduced to small vestigial processes characteristic of the Muscidae in general. The sixth sternite, *6s,* is asymmetrically developed, and broadens out dorsally, in the upper left hand side, to form a backwardly-bowed, expanded area; and the sixth sternite is situated immediately below the pregenital plate, having been "captured" by the latter. The sixth tergite, *6t,* and the pregenital plate, *7s* and *8s,* may form rather narrow transverse bands; and the area of the pregenital plate which represents the seventh sternite, *7s,* is reduced to a small imperfectly demarked area in the lower left side of the pregenital plate. The cerci, *ce,* and the surstyli, *st,* are short, broad, flattened plate-like structures in most Muscidae, and frequently have been mistaken for divided sternites when they become approximated medianly in the ventral region. In practically all of these diagnostic features, the Muscid *Ophyra leucostoma* shown in Fig. 27 is strikingly like the typical Muscids shown in Figs. 30 and 32, and differs very markedly from the typical Anthomyids shown in Figs. 23, 25, 34, etc., so that on the basis of the evidence furnished by the terminalia, *Ophyra* is a typical Muscid, not an Anthomyid, as it is assumed to be by Dipterists in general.

The terminal abdominal structures of the stablefly *Stomoxys calcitrans,* shown in Fig. 32 (compare also Fig. 33) are so strikingly similar to those of the housefly type shown in Fig. 30, that the evidence furnished by the terminalia is very clearly against the proposal of some recent Dipterists to raise the subfamily Stomoxydinae to family rank, apparently upon such trivial features as the development of piercing mouth parts, etc., in these Muscids; and the modern tendency to split the Cyclorrhapha into a myriad of "families" on the basis of trivial characters, which would at most be considered as merely of subfamily value (or even less) in other insects, has often been commented upon adversely by the more conservative taxonomists. Since the terminalia apparently furnish such extremely valuable evidence for determining the closest affinities of such Muscids as *Ophyra* and *Stomoxys,* etc., for a natural grouping of these flies, it is greatly to be hoped that the highly valuable evidence of the terminalia (which include the parts of at least seven segments) will also be taken into consideration in future attempts to classify these flies more accurately than is possible when such valuable evidence is disregarded.

While the terminalia apparently offer some very valuable clews for placing the Calypteratae in their proper family groups, it must be admitted that the terminal abdominal structures are of relatively little use in attempting to unite the Scatophagidae, Anthomyidae, Muscidae, etc., in a common superfamily Muscoidea (in the restricted sense) as distinguished from the Sarcophagidae, Calliphoridae and other forms sometimes grouped in the superfamily Tachinoidea, since all of these Calypteratae are very closely interrelated, and might be regarded as members of a single superfamily Muscoidea. It may be noted, however, that the sixth sternite, *6s,* of most Scatophagids (Fig. 18), Anthomyids (Figs. 10, 19, 31, etc.) and Muscids (Figs. 27, 30 and 32), lies directly under the pregenital plate, and its upper left hand region broadens out into a characteristically posteriorly-bowed area, while the sixth sternite, *6s,* of most of the other families (Figs. 38, 43, 45, 46, 48, 53, etc.) does not lie quite so directly under the pregenital plate, and is not bowed posteriorly in its upper left-hand region.

The typical Tachinidae shown in Figs. 36, 37 and 38 have a deeply cleft fifth sternite, *5s,* with well-developed copulatory lobes, *cl;* and in front of the pregenital plate, *7s* and *8s,* is a rather wide expanse of membrane which tends to "hump up" in the dorsal region, thereby causing the reduced pregenital plate to be pushed back, and tend to assume a slightly more horizontal position. This dorsal membranous region may contain the sixth tergite *6t* (as in Fig. 37), or the sixth tergite may apparently fade out into the membrane (as it appears to do in Fig. 38) ; and the sixth tergite *6t,* does not seem to unite with the pregenital plate when the latter remains reduced, although it may do so (Fig. 35) when the increasing sclerotization of the pregenital plate causes it to extend forward into the region of the sixth tergite—unless the sixth tergite fades out into the membrane before the pregenital plate encroaches upon its area.

The area of the seventh sternite, *7s,* of the Tachinids shown in

Figs. 36, 37 and 38, is imperfectly defined by a very faint superficial marking, which tends to extend upward into the dorsal region for a short distance, demarking a narrow incomplete marginal area along the anterior border of the pregenital plate. This area apparently corresponds to the anterior marginal region demarked in the pregenital plate, *8s,* of the Calliphorid *Cochliomyia,* shown in Fig. 53, and its appearance suggests that it may possibly be a vestige of the missing seventh tergite, although it seems more probable that it is merely a dorsal extension of the lateroverted seventh sternite, *7s,* if it is not merely a secondarily demarked anterior area of the pregenital plate, having no special significance.

Thelaira nigripes, shown in Fig. 38, is placed in the separate family Dexiidae, by some Dipterists, but *Thelaira* is remarkably similar to the Tachinid *Gonia capitata,* shown in Fig. 36, in which the sixth tergite has likewise become obliterated as in *Thelaira. Thelaira* also resembles the Tachinid *Euphorocera clavipennis,* shown in Fig. 37, which, unlike *Thelaira,* has retained its sixth tergite, *6t,* but in other respects is very like *Thelaira.* If *Thelaira* (Fig. 38), is a typical "Dexiid," and *Gonia* (Fig. 36) and *Euphorocera* (Fig. 37) are typical Tachinids, the differences between the two types of flies are scarcely even of subfamily value, much less of family value; and the evidence of the male terminalia would thus indicate that the so-called "Dexiidae" should be relegated to the status of a subfamily, Dexiinae, of the family Tachinidae.

Phorichaeta (Fig. 40) and *Cylindromyia* (Fig. 35) are usually classed as Tachinids by Dipterists, although they approach the Phasiids shown in Figs. 43 and 44 in the tendency for the curved dorsal area between the fifth tergite, *5t,* and the ninth tergite, *9t,* to become increasingly sclerotized, although it would appear that the increasing sclerotization does not spread from exactly the same centers in both cases, since it would appear that in the Tachinids shown in Figs. 40 and 35, the pregenital plate (bearing the labels *7s* and *8s*) increases at the expense of the area of the sixth tergite, *6t,* while in the more typical Phasiids shown in Figs. 43 and 44, the sclerotization of the sixth tergite, *6t,* likewise appears to increase in size, if the imperfectly demarked area, *6t,* bearing the sixth spiracle in Figs. 43 and 44, represents the sixth tergite. The occurrence of the sixth spiracle in the area in question in Figs. 43 and 44, may possibly be taken to indicate that this area, *6t,* represents the sixth tergite in this instance, but this is not necessarily so, as will be discussed later under the discussion of the occurrence of the spiracles in this region, and the secondarily-acquired symmetry exhibited by them.

The Phasiids *Trichopoda* and *Cistogaster* shown in Figs. 43 and 44, are characterized by the pronounced declivity of the region between the fifth and ninth tergites, *5t* and *9t,* and by the heavy sclerotization of this region, which is demarked into two areas here interpreted as the sixth tergite, *6t,* and the pregenital plate (bearing the labels *7s* and *8s*). The faint line between these two areas is here interpreted as the boundary between the sixth tergite and pregenital plate, because it extends between the spiracles of the sixth segment and seventh segment. These Phasiids resemble the Tachinids shown in Figs. 35 and 40, which serve to connect the Phasiids with the more typical Tachinids shown in Figs. 37 and 36, so that so far as the evidence of the male terminalia is concerned, the Phasiids were apparently descended more or less directly from Tachinid ancestors.

The so-called Megaprosopidae, represented by *Microphthalma disjuncta,* shown in Fig. 41, are too much like such Phasiids as *Cistogaster immaculata,* shown in Fig. 44, to be placed in a family distinct from that containing *Cistogaster.* Exactly the same type of declivitous, highly sclerotized area occurring between the fifth tergite, *6t,* and ninth tergite, *9t,* is found in both insects, and is divided by a faint line into a sixth tergite, *6t,* and a pregenital plate, *7s* and *8s,* in both insects; and the other differences are hardly of subfamily value, so that it is preferable to relegate the so-called family group Megaprosopidae to the rank of a subfamily of the Phasiidae, if the already sufficiently numerous "families" of Cyclorrhapha are to be kept within reasonable bounds.

The Gasterophilid *Gasterophilus intestinalis,* shown in Fig. 39, is sufficiently different from the other forms here described to warrant placing it in an entirely distinct family, the Gasterophilidae; and it appears to be as closely related to the Tachinoidea as any other group of flies here figured, although it has been placed in the family Muscidae by some recent Dipterists, while others place it in the Acalypterate group with the Sepsids, etc. The terminalia of *Gasterophilus* (Fig. 39) are clearly too different from those of typical Muscids (Figs. 30, 32, etc.) to warrant placing it in the family Muscidae, and the terminal structures of *Gasterophilus* (Fig. 39) are as much like those of the Tachinid *Cylindromyia binotata* (shown in Fig. 35) as any of the insects here described. There is no distinct sixth tergite or sternite in either of the insects shown in Figs. 39 and 35, and the pregenital plate, *7s* and *8s,* is rather declivitous in both, while the ninth tergite, *9t,* has a "bulging" contour in both insects, and the cerci, *ce,* and surstyli, *st,* are quite similar in both of these flies. Judging from the character of the terminalia, it is possible that the Gasterophilidae were descended from Tachinoid forebears somewhat like the Tachinid shown in Fig. 35; and the fact that the Tachinids tend to be parasitic would lend weight to the view that the parasitic Gasterophilids were possibly descended from Tachinoid forebears.

The cuterebrid *Cuterebra americana* (or *Atrypoderma americana* as it is called by recent Dipterists) shown in Fig. 42, resembles the Phasiid *Trichopoda pennipes,* shown in Fig. 43, in that the fifth sternite, *5s,* is not cleft posteriorly in either insect; and the pregenital plate is sharply declivitous in both of these flies, and these resemblances may possibly indicate that the Cuterebrids were descended from ancestors rather closely related to the Phasiidae.

It should be noted, however, that the pregenital plate, labeled *7s* and *8s* in Fig. 42 of *Cuterebra,* differs somewhat from the pregenital plate, labeled *6t, 7s* and *8s* in the Phasiid shown in Fig. 43, as is indicated by the location of its transverse sutures with relation to the position of the neighboring spiracles. In the Cuterebrid shown in Fig. 42, for example, the sixth spiracle is *not* borne in the pregenital plate as it is in Fig. 43; and this might possibly indicate that the sixth tergite has become atrophied in Fig. 42, instead of becoming large and uniting with the pregenital plate as it appears to do in Fig. 43, in which the area of the sixth tergite, *6t,* is demarked by an incomplete transverse suture (and faint impressed line) extending across the pregenital plate between the sixth and seventh spiracles, and lying *in front of* the seventh spiracle. In Fig. 42, on the other hand, the transverse suture extends *behind* the seventh spiracle, and this may indicate that the areas labeled *7s* and *8s* in Fig. 42 correspond only to the area labeled *7s* and *8s* in Fig. 43, in which a surface marking (indicated by a dotted line) extends across the pregenital plate in front of the seventh spiracle. The slight difference in the composition of the pregenital plate, however, would not necessarily preclude deriving the Cuterebrids and Phasiids from a common ancestry, and might merely indicate that both groups were possibly derived from Tachinoid ancestors (resembling the Tachinid shown in Fig. 37 to some extent).

The pregenital plate, labeled *6t, 7s* and *8s* in the Phasiid shown in Fig. 43, exhibits a *secondarily*-acquired bilateral symmetry (even with respect to the occurrence of the sixth and seventh spiracles on both sides of the body), which results in a deceptive masking of the torsion of the parts, externally. By tracing the modifications of the pregenital plate of the Phasiid shown in Fig. 43 back to its prototype in the Tachinid shown in Fig. 37, and through this Tachinid to the type of pregenital plate occurring in the ancestral Anthomyid shown in Fig. 23, we may logically conclude, however, that the terminalia of the Phasiid shown in Fig. 43 underwent a previous torsion of the parts before they finally acquired a secondary symmetry, as the end-result of the parts accommodating themselves to each other, as they settled down in their final adjustment, and became more or less rigidly set, after acquiring a *secondary* external symmetry.

Although the occurrence of the sixth and seventh spiracles in or near the pregenital plate may be of some significance for indicating the components of the pregenital plate in some cases, too much weight cannot be given to the occurrence of these spiracles, as is shown in the following instances.

In the Phasiid shown in Fig. 44, the sixth spiracle enters the enlarged sclerite forming the pregenital plate (labeled *6t, 7s* and *8s*) when the sixth tergite, *6t,* combines with the enlarged pregenital plate; but in Fig. 41, the sixth spiracle does not enter the pregenital plate, when the sixth tergite, *6t,* combines with it. In Fig. 50, on the other hand, the sixth spiracle enters the pregenital plate despite the fact that the sixth tergite, *6t,* remains distinct from the pregenital plate; and in such instances as these, the comparative morphology of the sclerites furnishes a better guide than the occurrence of the spiracles, for determining the composition of the pregenital plate.

It may also be noted that in the Tachinid shown in Fig. 35 both the sixth and the seventh spiracles are borne in the enlarged pregenital plate, labeled *7s* and *8s* (compare also Figs. 7, 29, 44 and 50), while in the Tachinid shown in Fig. 38, on the other hand, both of these spiracles lie in the membrane in front of the pregenital plate (compare also Figs. 9, 13, 33, etc.), and still another condition is exhibited by the spiracles in the Tachinid shown in Fig. 36, in which the seventh spiracle is borne in the pregenital plate, while the sixth spiracle lies in the membrane in front of the pregenital plate—as is also the case in most of the Diptera here discussed (e.g., Figs. 42, 23, etc.).

From the foregoing discussion, it is evident that the occurrence of the sixth spiracle in the enlarged pregenital plate really indicates that the sixth tergite also enters into the composition of the pregenital plate only when the comparative morphology of the parts likewise confirms it (as in Figs. 43 and 44), for the sixth spiracle may enter the pregenital plate while the sixth tergite lags behind (as in Fig. 50), or the sixth tergite may even combine with the pregenital plate while the sixth spiracle lags behind (as in Fig. 41); and all possible combinations of the occurrence of the sixth and seventh spiracles with reference to the pregenital plate are found in the Tachinids shown in Figs. 35, 36 and 38, so that in this case, as in most other instances as well, the comparative morphology of the sclerites is the only safe guide for interpreting the parts of the male terminalia.

It is rather difficult to characterize the Sarcophagidae on the basis of their terminalia; and the terminal abdominal structures do not furnish many features of value for definitely determining the closest affinities of the Sarcophagids.

Sarcophagids such as the one shown in Fig 20 (compare also Fig. 45) have an elongated horizontal pregenital plate (labeled *7s* and *8s*) in which the sinistral seventh spiracle is borne far back toward the middle of the pregenital plate, thus suggesting that the seventh sternite, *7s,* forms a large portion of the pregenital plate, as it likewise appears to do in the Cordylurids shown in Figs. 17 and 16; but in the Sarcophagid shown in Fig. 47, the pregenital plate is more vertical, and is not so greatly elongated as it is in the other Sarcophagids here figured.

The Sarcophagids differ from many other Calypterate families in having the surstyli, *st* of Figs. 45 and 47, reduced and situated under the ventral border of the ninth tergite, *9t,* resembling such Tachinids as the one shown in Fig. 36, in this respect. Sarcophagids such as the one shown in Fig. 20 likewise resemble such Tachinids as the one shown in Fig. 36 in exhibiting a tendency for the membranous region in front of the pregenital plate, *7s* and *8s,* to become enlarged and bulging dorsally, and for the sixth tergite to become obliterated in this region. Sarcophagids such as the one shown in Fig. 45, on the other hand, resemble Calliphorids, such as the one shown in Fig. 46, in the general appearance of the ninth tergite, and other features as well; but the resemblances are not very striking, and the closest affinities of the Sarcophagids are rather obscure.

In typical Calliphorids, such as those shown in Figs. 48 to 53, the fifth sternite, *5s,* is cleft posteriorly—as is also the case in many other Calypteratae. The sixth tergite, *6t,* is usually well developed in the Calliphoridae, and tends to extend over the pregenital plate, *7s* and *8s,* which forms an angle with it in such Calliphorids as those shown in Figs. 48 and 53, in which the angle thus formed causes the terminalia to bulge out in the dorsal region.

The surstyli, *st,* of the Calliphorids are pointed structures, suggestive of those of the Anthomyids, particularly in the Calliphorid shown in Fig. 46, in which the surstyli, *st,* are long and slender, and the parts of the terminalia are very like those of the Anthomyid shown in Fig. 28. In the form and position of its surstyli, *st,* and in the general appearance of the ninth tergite, *9t,* the Calliphorid shown in Fig. 46, likewise resembles the Sarcophagid shown in Fig. 45.

Many Dipterists consider that the Calliphorids are so closely related to the Muscids that they place the Calliphorids in a subfamily, Calliphorinae, of the family Muscidae; but the terminalia of male Calliphorids apparently point to a somewhat closer relationship to the Anthomyids, from which the Muscids arose. Typical Calliphorids, such as those shown in Figs. 48 to 53, differ from the typical Muscids shown in Figs. 30 and 32, in the following respects. The fifth sternite, *5s,* is cleft posteriorly, and the sixth sternite, *6s,* is not bowed posteriorly in its upper left-hand region in the Calliphorids (Figs. 48 to 53), while in the Muscids shown in Figs. 30 and 32, the fifth sternite, *5s,* is not cleft posteriorly, and the sixth sternite, *6s,* is bowed posteriorly in its upper left-hand region. The cerci, *ce,* and surstyli, *st,* of the Calliphorids (Figs. 38 to 53) are slender, and taper to a point distally, while in the Muscids shown in Figs. 30 and 32, the cerci, *ce,* and surstyli, *st,* tend to become broad and flat, and do not taper distally. In these features the Calliphorids appear to be somewhat closer to the Anthomyidae than they are to the Muscidae, and also resemble the Sarcophagidae and Tachinidae in them. In fact, the lines of descent of the Muscidae, Anthomyidae, Calliphoridae, Sarcophagidae and Tachinidae all intergrade so intimately that it is extremely difficult to determine whether the Calliphoridae and Sarcophagidae should be grouped in the superfamily Muscoidea (in the restricted sense) or in the superfamily Tachinoidea (or "Larvaeovoroidea"), and the writer's former suggestion (Crampton, 1942, p. 118) to place the Calliphoridae and Sarcophagidae in the superfamily "Larvaeovoroidea" is admittedly open to some objection from this standpoint.

The principal external features of the terminalia of typical male Calypterate Cyclorrhapha are illustrated fairly well by the Calliphorid *Phormia regina* shown in Fig. 11 (compare also Fig. 34), while the details of the internal structures in the neighborhood of the aedeagus are illustrated by the Calliphorids shown in Figs. 49, 52 and 54.

As is shown in Figs. 11 and 34, the fifth abdominal segment is usually the last segment of the preabdomen in male Calypteratae. In the preabdomen of male Calypteratae, the spiracles are usually (though not always) borne in the ventro-lateral region of the tergites, while in the preabdomen of male Acalypteratae they are usually located in the lateral membrane below the tergites. In the postabdomen of male Cyclorrhapha in general, the sinistral sixth spiracle is usually located in the lateral membrane, and the sinistral seventh spiracle is usually borne in the pregenital plate, although exceptions to this rule have already been pointed out.

The fifth sternite is frequently cleft posteriorly in male Calypteratae (but only rarely in male Acalypteratae), and the copulatory lobes which it bears usually project posteriorly below the aedeagus, as far back as the bases of the cerci. The aedeagus, *ae* of Figs. 52 and 17, is usually thrust forward into a genital pouch, or cubiculum, *cu,* for protection, in repose.

The slender sixth sternite, *6s* of Figs. 24, 34 and 52, which is frequently asymmetrically developed, loops downward around the opening of the cubiculum, *cu* of Fig. 52, to support its membranous walls; and the roof of the cubiculum is supported by the hypandrial apodeme, *ha* of Figs. 52 and 49, which is formed by an inflexion of the ninth sternite, *9s* of Fig. 49. Above the hypandrial apodeme, *ha* of Figs. 52, 54 and 49, lies the aedeagal apodeme, *aa,* which is attached to the intermediate plate (labeled *i* in Fig. 49) located at the base of the aedeagus, *ba;* and this intermediate plate lies between the bases of the anterior gonapophyses, or pregonites, labeled *a* in Figs. 49, 54, etc. The muscles attached to the aedeagal apodeme aid in retracting the aedeagus.

On each side of the aedeagus, *ae,* lie the paired pregonites and postgonites, *a* and *b* of Figs. 49, 54, 34, etc., commonly called the anterior and posterior gonapophyses. The latter terms, however, are likewise applied to the anterior and posterior valves of the ovipositor in Orthopteroid insects, which are not homologous with the anterior and posterior gonapophyses of male Cyclorrhapha; and in order to avoid the confusion attendant upon applying the same terms to two wholly different sets of structures, it is preferable to designate the so-called anterior and posterior gonapophyses of male Diptera as the pregonites and postgonites (*a* and *b* of Figs. 49, 54, 34, 11, etc.). These "gonites" of male Cyclorrhapha may be homologous with somewhat similar structures occurring in the males of such lower Brachycera as the Stratiomyidae, Therevidae, etc., or the gonites may be structures more or less peculiar to male Cyclorrhapha, and develop to aid in holding the parts together in mating (by fitting into certain pockets in the female terminalia) as the forcipate claspers (or parameres) of the lower Diptera become atrophied, or are unrecognizably transformed.

The aedeagus, *ae,* of many Calliphorids, etc., is subdivided into two regions called the basaedeagus, and the distaedeagus, labeled *ba* and *da* in Figs. 49 and 54. A genital spine, called the gonacanthus or epiphallus, *c,* projects from the basal portion of the aedeagus, *ba,* in Figs. 34 and 54; and in many Calliphorids, the distal portion of the aedeagus bears processes called the hypophallus, paraphallus and acrophallus (labeled *hp, pp* and *ap* in Fig. 54), most of these terms being taken from Lowne's monumental work on the blowfly *Calliphora erythrocephala.*

Paired sperm ducts conduct the spermatozoa from the testes, *ts* of Fig. 54, to the common duct, which also receives the products of the paragonia, *pa,* whose thickened secretions, according to Lowne (1893–95), serve to bind together the spermatozoa, when they are discharged through the ejaculatory duct, *ed,* by the action of the sperm syringe, or ejaculator, *sp.* An ejaculatory sclerite, embedded in the walls of the ejaculator, *sp* of Fig. 54, furnishes attachment for the circular muscles extending around the syringe; and the contraction of these muscles serves to drive the semen through the ejaculatory duct, and out of the aedeagus, in copula. Apparently, the ejaculatory duct, *ed* of Fig. 54 (or the continuation of the common sperm duct), loops up from left to right over the top of the hindgut in all male Cyclorrhapha (including the Syrphoidea), and it is probable that a similar condition will be found to exist in the males of the Orthorrhaphous Brachycera, such as the Bombyliidae, Cyrtidae, Phoridae, Lonchopteridae, etc., which approach the ancestral Syrphoid stock of the Cyclorrhapha.

In male Calypteratae, the external evidence of the clockwise torsion of the terminalia is largely restricted to the oblique arrangement of the asymmetrical sixth, lateroverted seventh, and inverted eighth abdominal sternites, *6s, 7s* and *8s,* occurring in such primitive Anthomyids as the ones shown in Figs. 23, 10, 19, etc. (compare also Fig. 9), although the ninth segment, which undergoes a still more violent twist or circumversion, does not present any visible external evidence of the torsion it undergoes before coming to rest in its final position. In many higher Calypteratae, the extent of the former oblique twist of the segments preceding the ninth is later concealed when the reduced lateroverted seventh sternite merges with the inverted eighth sternite to form the composite pregenital plate, which eventually assumes a symmetrical appearance even in the arrangement of the spiracles it bears, although it is not symmetrical in such primitive Calypteratae as the ancestral Anthomyids shown in Figs. 23, 10, etc.

The appendages, *st,* of the ninth tergite, *9t,* of the Calliphorids shown in Figs. 54, 52, 51, etc., are called the surstyli or edita. Together with the cerci, *ce,* they serve to aid in holding the parts of the female in mating, or, extending forward below the aedeagus, they likewise serve to protect this delicate organ when it is thrust into the cubiculum in repose. The connecting rods, *cr* of Fig. 49, extending backward from the posterior region of the ninth sternite, *9s,* to the bases of the surstyli, *st,* cause them to become flexed when the muscles attached to the hypandrial apodeme, *ha,* draw the ninth sternite forward. The surstyli have been interpreted as parts of the modified genital forceps of the lower Diptera by some investigators, but are tergal structures borne on the ninth tergite, *9t,* while the genital forceps are sternal structures borne on the ninth sternite, and the two different types of structures cannot be homologous.

The cerci, *ce,* are the modified limbs of the eleventh segment, which unites with the tenth segment to form the proctiger, or anus-bearing segmental complex, *pg* of Figs. 54 and 52. The cercus-bearing eleventh segment unites with the tenth segment in male Mecoptera, which are very like the ancestors of the Diptera; and in many male Orthopteroid insects, which are like the ancestors of the Holometabola in general, the cercus-bearing eleventh segment unites with the tenth segment, so that it is not at all surprising that the same thing has occurred in male Diptera, although some investigators do not consider that the cerci of male Diptera are actually such, since they appear to be borne on the tenth "segment," which, however, is a composite "segment" composed of the united tenth and cercus-bearing eleventh segments, as is also the case in the above-mentioned male Mecoptera and Orthopteroid insects. In some Calypteratae the cerci unite ventrally to form a single plate or zygocerci; but they are usually distinct in most male Cyclorrhapha.

The cerci bear sensory organs, and, together with the surstyli, may serve as accessory clasping organs in copulation. The cerci and surstyli usually operate together, and have even been interpreted as parts of the same structure, although the cerci are appendages of the eleventh segment (embryologically), while the surstyli are processes of the ninth tergite. The cerci and surstyli usually extend forward under the aedeagus in repose (when the latter is thrust into the cubiculum), and the copulatory lobes of the fifth sternite extend backward beneath them only as far as the bases of the cerci, to leave the anal opening free at all times for the unimpeded discharge of the faeces.

The grouping of the families of the Calypteratae suggested by the study of the male terminalia may be briefly indicated by dividing the Calypteratae (or Muscamorpha as they may be called) into two principal superfamilies—to which two other minor superfamilies might possibly be added.

The first main superfamily, the Muscoidea (in the restricted sense), contains the families Scatophagidae, Glossinidae (of doubtful affinities), Anthomyiidae, and Muscidae. The Sarcophagidae and Calliphoridae are also grouped in this superfamily by some Dipterists, such as Townsend, but the writer is inclined to group these two families in the Tachinoidea (or "Larvaeovoroidea"), although the ultimate disposal of the Sarcophagidae and Calliphoridae cannot be definitely determined in the present state of our knowledge.

If the Cordyluridae are to be regarded as true Muscomorpha, or Calypteratae, as most modern Dipterists maintain, it might be advisable to place them in a separate superfamily, the Cordyluroidea. Their terminal abdominal structures, at any rate, would indicate that they are sufficiently different from the Muscidae to be placed in a distinct family, although Curran (1934, North American Diptera) places them in the family Muscidae.

The second main superfamily, the Tachinoidea (or Larvaeovoroidea), includes the Tachinidae and Phasiidae, with which the Sarcophagidae and Calliphoridae might eventually be grouped, but for the present, it is preferable to suspend judgment concerning the closest affinities of the Sarcophagidae and Calliphoridae.

The Gasterophilidae and Cuterebridae resemble the Tachinidae very closely, and might be grouped in the superfamily Tachinoidea, although the genitalic differences might be considered sufficient to place them in a separate Oestroid superfamily.

From the foregoing discussion, it is evident that the study of the male terminalia is of considerable value for placing an insect in its proper family, and in some instances, it is also of value for grouping the families into superfamilies. Evidence of this type, however, has been much neglected by recent students of the Diptera, and it is greatly to be hoped that more attention will be given to this promising field when the present distractions of totalitarian war are past, and the younger Dipterists are free once more to devote their thoughts and energies to the solving of problems such as these!

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ABBREVIATIONS.

a	pregonite (anterior gonapophysis)
aa	aedeagal apodeme
ae	aedeagus
ap	acrophallus
b	postgonite (posterior gonapophysis)
ba	basaedeagus
bm	basimere or basistyle (basal segment of paramere)
c	epiphallus or gonacanthus
ce	cerci
cl	copulatory lobes of fifth sternite (copulalobi)
cl	jugobaculi or connecting rods
cu	cubiculum or genital pouch

da .... distaedeagus
dm .... distimere or dististyle (distal segment of paramere)

ha .... hypandrial apodeme
hp .... hypophallus

i .... intergonite or intermediate plate of gonites

pa .... paragonia
pg .... proctiger
pp .... paraphallus

s .... sternite (written after Arabic numeral denoting abdominal segment)
sp .... sperm syringe or ejaculator
st .... surstyli or edita

t .... tergite (written after Arabic numeral denoting abdominal segment)
ts .... testis

EXPLANATION OF FIGURES.

Unless otherwise stated, all figures are lateral views of the male terminalia viewed from the insect's left side.

Fig. 1. A Tipulid, *Cladura flavoferruginea.*
Fig. 2. A Stratiomyid, *Ptecticus* sp.
Fig. 3. A Syrphid, *Heliophilus chaligosa.*
Fig. 4. A Syrphid, *Sericomyia chrysotoxoides.*
Fig. 5. A Syrphid, *Baccha cognata.*
Fig. 6. A Syrphid, *Paragus bicolor.*
Fig. 7. A Clusiid, *Clusia lateralis.*
Fig. 8. A Helomyzid, *Neoleria crassipes.*
Fig. 9. A Helomyzid, *Anorostoma marginata.*
Fig. 10. An Anthomyiid, *Eremomyoides cylindrica.*
Fig. 11. A Calliphorid, *Phormia regina.*
Fig. 12. A Neriid, *Glyphidops filosus.*
Fig. 13. A Calobatid, *Mimegralla* sp.
Fig. 14. A Calobatid, *Calobata pallipes.*
Fig. 15. A Micropezid, *Micropeza* sp.
Fig. 16. A Cordylurid, *Parallelomma* sp. No. 1.
Fig. 17. A Cordylurid, *Parallelomma* sp. No. 2.
Fig. 18. A Scatophagid, *Scatophaga stercoraria.*
Fig. 19. An Anthomyiid, *Pegomyia lipsia.*

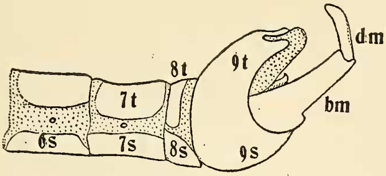
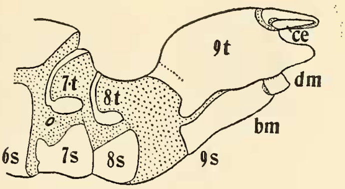


Fig. 1



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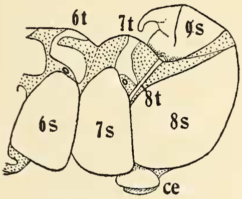

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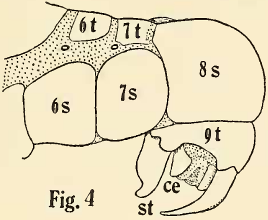

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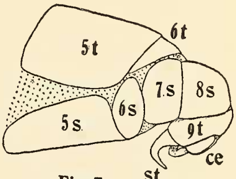

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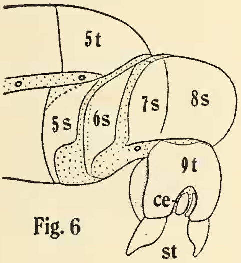

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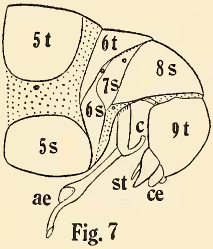

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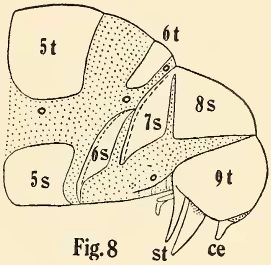

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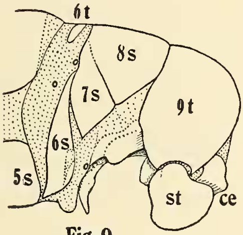


Fig. 9

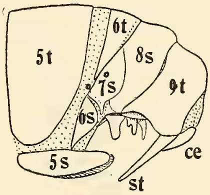


Fig. 10

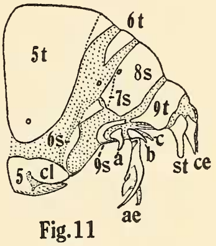


Fig. 11

Fig. 20. A Sarcophagid, *Sarcophaga haemorrhoidalis.*
Fig. 21. A Scatophagid, *Scopeuma furcata.*
Fig. 22. A Glossinid, *Glossina* sp.
Fig. 23. An Anthomyiid, *Protohylemyia* (*Hylemyia*) *spiniventris.*
Fig. 24. An Anthomyiid, *Macrorchis ausoba.*
Fig. 25. An Anthomyid, *Macrorchis ausoba.*
Fig. 26. An Anthomyiid, *Phaonia nigricans.*
Fig. 27. A Muscid, *Ophyra leucostoma.*

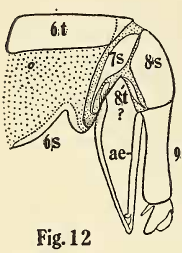
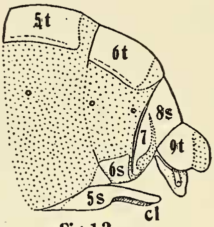


Fig. 12



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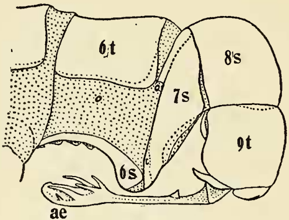

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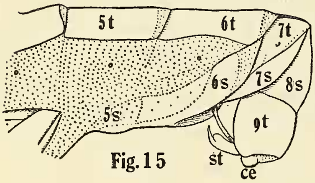

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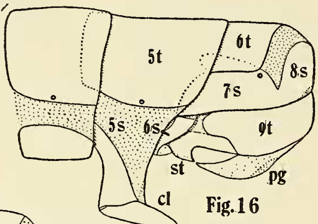

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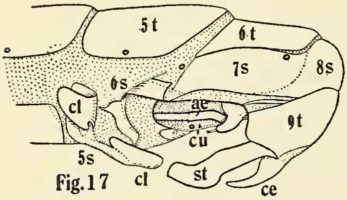

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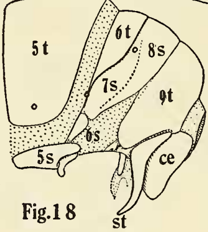

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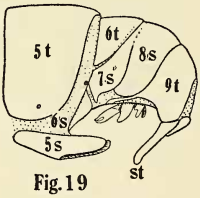

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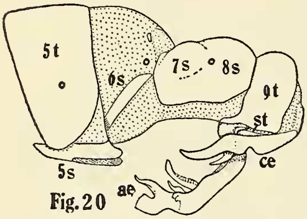

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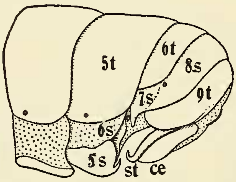

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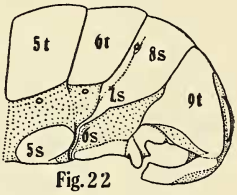
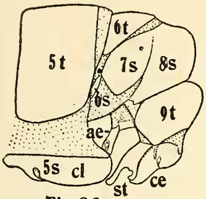


Fig. 22

Fig. 28. An Anthomyiid, *Paregle cinerella.*
Fig. 29. An Anthomyiid, *Fannia canicularis.*
Fig. 30. A Muscid, *Musca domestica.*
Fig. 31. An Anthomyiid, *Limosia errans.*
Fig. 32. A Muscid, *Stomoxys calcitrans.*
Fig. 33. A Muscid, *Lyperosia irritans* (*Haematobia serrata*).
Fig. 34. An Anthomyiid, *Hylemyia antiqua.*
Fig. 35. A Tachinid (Larvaeovorid), *Cylindromyia binotata.*
Fig. 36. A Tachinid, *Gonia capitata.*



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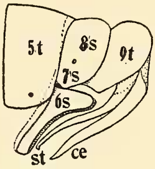

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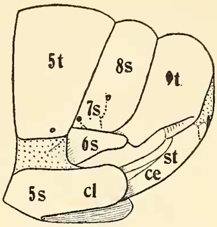

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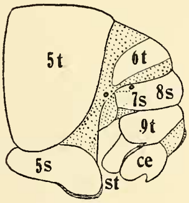

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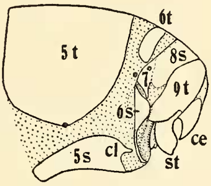

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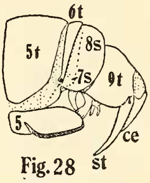

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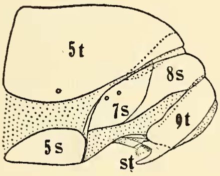

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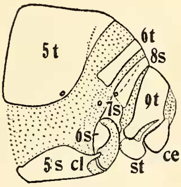

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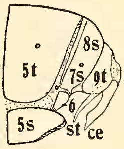

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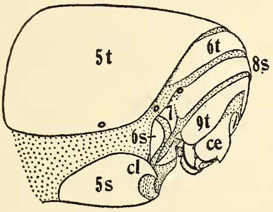

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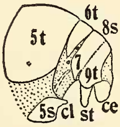

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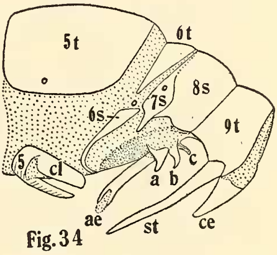
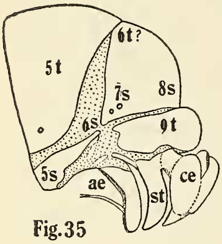


Fig. 34

Fig. 37. A Tachinid, *Euphorocera claripennis.*
Fig. 38. A Tachinid, *Thelaira nigripes.*
Fig. 39. A Gasterophilid, *Gasterophilus intestinalis.*
Fig. 40. A Tachinid, *Phorichaeta sequax.*
Fig. 41. A Phasiid, *Microphthalma disjuncta.*
Fig. 42. A Cuterebrid, *Atrypoderma* (*Cuterebra*) *americana.*
Fig. 43. A Phasiid, *Trichopoda pennipes.*
Fig. 44. A Phasiid, *Cistogaster immaculata.*



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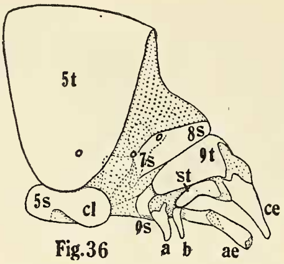

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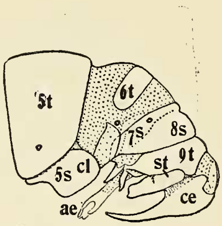

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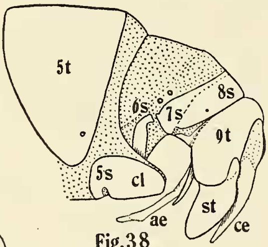

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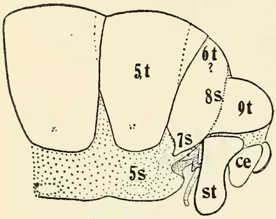

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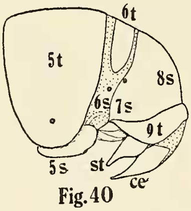

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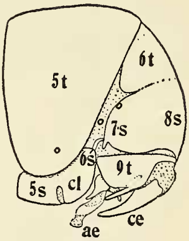

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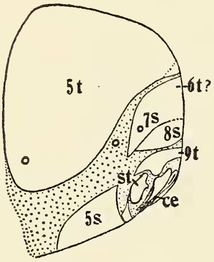

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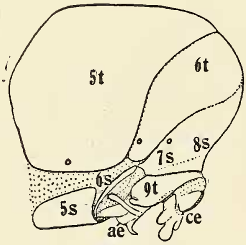

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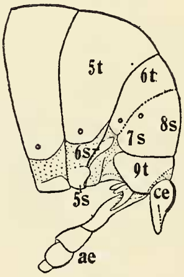


Fig. 44

Fig. 45. A Sarcophagid, *Boettcheria latisterna.*
Fig. 46. A Calliphorid, *Cynomyia cadaverina.*
Fig. 47. A Sarcophagid, *Ravinia peniculata.*
Fig. 48. A Calliphorid, *Protophormia terraenovae.*
Fig. 49. A Calliphorid, *Phormia regina* (ventral view).
Fig. 50. A Calliphorid, *Calliphora erythrocephala.*
Fig. 51. A Calliphorid, *Lucilia illustris.*

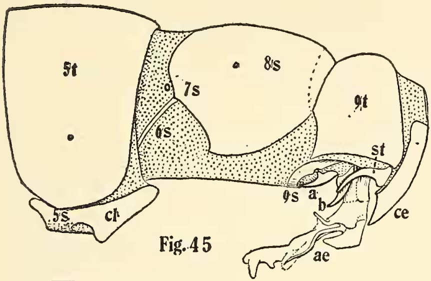


Fig. 45

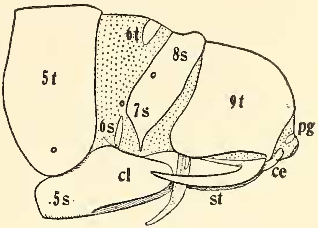


Fig. 46

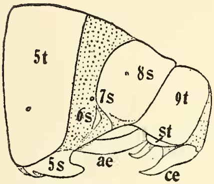
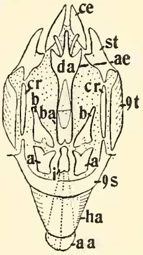


Fig. 47



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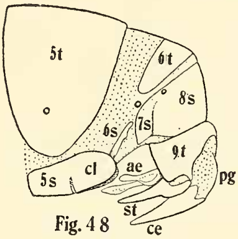

Fig. 48

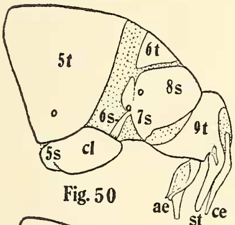

Fig. 50

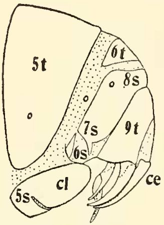

Fig. 51

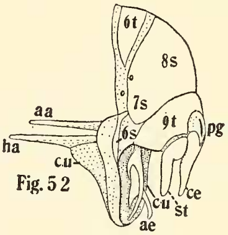

Fig. 52

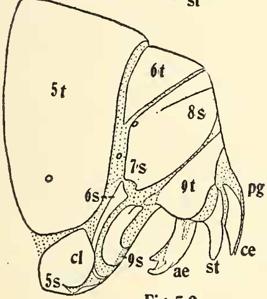

Fig. 53

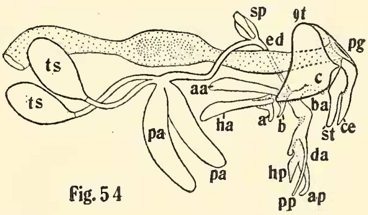

Fig. 54

Fig. 52. A Calliphorid, *Pollenia rudis.*

Fig. 53. A Calliphorid, *Cochliomyia americana.*

Fig. 54. A Calliphorid, *Phormia regina* (internal view of reproductive organs, showing looping up of ejaculatory duct over the top of the hindgut).